INCOMPATIBILITY OF MUTANT RACES IN DROSOPHILA

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Perhaps the most characteristic difference between ordinary mutant races in the laboratory or experimental garden, and incipient species in nature, is the difference in their ability to hybridize. Mutant races usually exhibit complete inter-fertility, while species, as a rule, are inter-sterile. If this distinction, based on fertility of mutants, were found to be a fundamental one (i.e., of universal application) it would offer a serious objection to the hypothesis of evolution through mutations, but, conversely, if it were not found to hold universally the objection would be removed or greatly minimized. The accompanying observations seem to indicate that the distinction does not hold universally.

In our cultures of Drosophila two cases have arisen in which mutant races exhibit an incompatibility that is indistinguishable, so far as we can see, from that found in nature between distinct species.[1] One of our cases appeared in cultures of Drosophila virilis at Cold Spring Harbor, the other in cultures of Drosophila melanogaster (ampelophila) at Columbia University.[2] Each case involves two mutants (apparently allelomorphs) that either refuse to cross or else give sterile hybrids— a situation comparable to that in the familiar case of the ass and horse. The essential data from out experiments are as follows:

1. *In Drosophila Virilis.*—Among eight sex-linked mutant characters in this species are two called 'glazed' and 'rugose,' that appeared independently, but almost simultaneously, over a year ago. Pure stock of each race breeds readily, and in this form both have been kept in the laboratory for over fifteen generations; likewise, each has been crossed with several other mutants as well as with the normal, and has shown a high degree of fertility in all cases. But when mated together their

behavior is very different; 'glazed' females by 'rugose' males have entirely
failed to give offspring, and the reciprocal cross, although easily ob-
tained, gives sterile hybrids (i.e., sterile females—these being the only
hybrid individuals). In other words, it has been impossible thus far to
get an F_2 generation from the cross, no matter how the mating was made.

No accurate record has been kept of the earlier experiments with the
two forms, but at least a score or more of matings were made at different
intervals during six or eight generations. Among the more recent at-
tempts, in which a record was kept of all F_1 matings, the following may
be cited: One experiment began with about a dozen reciprocal matings
between glazed and rugose, using several flies in each bottle. At least
three of these, in which glazed males and rugose females were used, gave
many offspring. Fourteen large, vigorous females were selected from
the latter and mated singly to several males—eight to rugose males, six
to normal males. They were all given the best possible cultural condi-
tions and treated exactly like other mutants of various kinds that were
mated at the same time. Practically all of the latter gave abundant
progeny, but not a single offspring appeared in any of the fourteen bottles
containing glazed-rugose hybrids, though the flies lived for a long time
(much longer than the ordinary length of one generation). Another
experiment was made in a different way. This time females hetero-
zygous for glazed were mated to rugose males, and females heterozygous
for rugose were mated to glazed males. These gave daughters half of
which were heterozygous for *either* rugose or glazed, and half of which
were heterozygous for *both* rugose and glazed. Forty-five females from
such cultures were mated singly to various males (mostly normal).
Twenty of the females were from the first mating, twenty-five from the
second. Out of the twenty females nine gave abundant offspring and
eleven gave none; out of the twenty-five females fourteen gave offspring,
eleven gave none; or, out of the total of forty-five, twenty-three gave
offspring and twenty-two did not. In three cases the female died before
the records were made, so the numbers are subject to that much error,
but in all of the others the flies lived to twice or three times the age at
which offspring are ordinarily produced. Of the twenty-three females
that did give progeny, every one proved to be heterozygous for only one
of the characters concerned—i.e., those from the first mating were hetero-
zygous for rugose but not glazed; those from the second mating were
heterozygous for glazed but not rugose—leaving no doubt that the sterile
females were those carrying both glazed and rugose.

It is difficult to avoid the conclusion that we are dealing here with a
complete, or at least a high degree of incompatibility. That it is spe-

cific for the two mutants in question, and is not an ordinary case of sterility, is shown by the fact that both mutants are fertile and give fertile hybrids with other mutants and with the normal. Furthermore, the sterility of the hybrids in question is in no way dependent upon the males used, at least so far as normal, rugose and glazed are concerned, for all three kinds have been tried.

2. *In Drosophila Melanogaster (Ampelophila)*.—The case found in *D. melanogaster* may be summarized as follows: A mutant form, 'notch' wing, crossed to the fully fertile mutant 'facet' eye, gave F_1 hybrids which were completely sterile with the common parent type and with one of the mutant forms, facet.

The sex-linked mutant, notch, is principally characterized by a notch of definite type but variable extent in the tip of the wing. Notch is dominant in the female, and in the male acts as a lethal. The locus of notch was found to be at approximately 2.6.[3] In an attempt to locate the gene for notch more accurately, it was decided to use in a linkage experiment the recessive mutation facet[3] whose locus had been found to be at approximately 2.2, very close to the supposed position of notch. Accordingly, when notch reappeared (December, 1915), the single notch female, which appeared as a mutation in a pedigreed culture, was mated to yellow facet males (yellow is a recessive body color whose locus is at 0.0).

The F_1 generation furnished a surprise, for every one of the daughters that was notch was also facet! Two explanations of this peculiar 'compounding' of notch and facet are open to us: either the notch mutation is a deficiency[4] for facet, or the two mutant forms are allelomorphic.

It had been the intention to backcross a number of the expected F_1 notch females to yellow facet males in order to secure sufficient linkage data upon the relative positions of these factors. When it was found that facet showed an apparent dominance with notch this plan presented difficulties. Nevertheless, nine of the notch-facet daughters were mated to yellow facet males as originally planned, while six more were mated to yellow notch-facet males. *Not one of these fifteen females produced offspring.* It was then realized that this relation was unusual, and a second effort was made to secure offspring. Fresh males were given to the remaining females (three having died) and they were transferred to fresh culture bottles. The discarded parent bottle was also rescued and three additional notch-facet females—the last to hatch—were secured and likewise mated to yellow facet males. No offspring were produced. Since the death of these females 'without issue' would mean the loss of the mutation and would shut the door on the solution

of the problem, a third, but equally unsuccessful, effort was made by transferring such females as were still alive to fresh culture bottles.

So many matings were attempted that it is impossible to regard their failure as accidental or as due to poor cultural conditions. It must be considered established that the fertility of the notch-facet hybrid was of a different order from that of either parent race.

Notch has reappeared on at least three other occasions, and in one of these cases the facet test has been made. The new notch-facet test gave the peculiar notch-facet compound, but this compound was fully fertile. The original facet cross had been made to a notch which arose by a separate and independent mutation, and was probably not identical with the notch of the later test but was an allelomorph. The original notch seemed to be a somewhat more extreme type than the others. Furthermore, a parallel case (in D. melanogaster) has been found, in which two allelomorphs that differ little in appearance differ markedly in their fertility relations. The mutation lethal 2 gave an aberrant linkage result[3] which led to tests for deficiency by mating lethal 2 females to males of mutations whose loci were known to be close to that of lethal 2. In the test by the recessive 'club' the same apparent dominance was found as in the case of notch-facet;—that is, females heterozygous for lethal 2 mated to club males gave half the daughters club and half normal, and it was easy to demonstrate that the ones that were club were also the ones that were lethal 2, for these lethal 2-club hybrids were fertile. In other crosses not involving club very rarely a male having the lethal 2 gene was able to hatch, and these males, which showed all the characteristics of club, were completely sterile.

3. If we imagine such cases as these to occur in nature it is evident that they might be of evolutionary significance. For instance, suppose that the two mutants 'glazed' and 'rugose' of D. virilis appeared in the wild state. Their establishment would depend, of course, upon the viability of the mutants, and in this particular instance one of them (glazed) would probably be eliminated, although the other, judging from its vigor, would stand a good chance of surviving. But the consideration of viability need not affect the case as an illustration, for it must be assumed *a priori* that any variants, to be of evolutionary significance, must be viable. Supposing, then, that the two mutants in question appeared as viable forms in nature; the result would be a composite species consisting of three types, two of which were fertile with the third but infertile with one another. If for any reason the third type (in this case the normal) were to be eliminated, the first two would become distinct species, even though they differed in only one or two external characters to begin with.

This scheme involves an obvious difficulty, in that it assumes the elimination of what would probably be the most numerous and wide-spread of the three types—the normal or parent type—while the probabilities greatly favor the elimination of one or both mutant types. If we slightly alter the conditions of the case, however, the difficulty is reduced. Supposing that instead of the two mutant races arising from the normal stock, only one (a) has this origin, while the second (b) is derived in turn from the first one, and that, instead of the two mutants being incompatible with each other, the second is incompatible with the normal. In this case the first mutant (a) acts simply as an intermediate step between the two incompatible forms, normal and mutant (b), and if it is eliminated the other two stand as distinct species. Here we have a case which differs in no essential respect from the former, but which is less improbable in that it involves the elimination of one of the mutant forms instead of the more widespread parent stock.

The same sort of scheme applies equally well to the case in D. melanogaster, so far as illustrative purposes are concerned. In this particular instance it happens that one of the mutant characters (notch) is a dominant that cannot be obtained in a homozygous condition because of its lethal effect, and hence the mutant could never make a pure race; but there is no necessary connection between lethal action and incompatibility.

In connection with these experimental data it is interesting to note two other lines of evidence, taken directly from wild flies. First, with respect to the question of whether or not mutant races can survive in nature, it may be recalled that the possibility of such survival is practically demonstrated by such cases as that described by Sturtevant in Drosophila repleta.[5] Two forms of this fly are found existing side by side in the wild state, and one of them is a typical sex-linked recessive to the other. There is every reason to believe that one of these has arisen from the other by mutation, and bears the same relation to it that any one of the above mutants does to the normal of its species. If we suppose that either of these forms in D. repleta gives rise to a third form that is incompatible with the other, and then becomes eliminated itself, we have all of the necessary steps in the formation of a new species; and the case differs in no essential respect from the hypothetical ones outlined above.

Another line of evidence (also from D. repleta) bears more especially upon the question of incompatibility in wild races. Here, instead of two wild forms that interbreed freely but are unlike in appearance, we have two varieties that refuse to interbreed, but are extremely similar in

appearance. They are so similar, indeed, that it is very doubtful whether they would have been recognized, even as varieties, if cytological examination had not shown them to differ in respect to their chromosomes,[6] and if they had not been bred in the laboratory to test their compatibility. Here is an apparently clear case of incipient species formation. It seems practically certain that these two varieties, or species, have had a common origin, and that their individuality at the present time is due mainly to their incompatibility. Either of them would, in our opinion, pass for a mutant race of the other; and it is not difficult to imagine that they might have become differentiated from one anther in some such way as that outlined above; i.e., by mutations that brought about incompatibility. With the incompatibility once established they are now free to diverge more and more until they become clearly differentiated from one another.

4. To recapitulate: The evidence from two cases of incompatibility between mutants in laboratory cultures, together with evidence from what appear to be mutant forms and incompatible varieties in nature, tends to remove one of the most serious objections to the mutation hypothesis, and lays emphasis upon the possible evolutionary importance of mutations involving incompatibility.

[1] In each case the two respective mutants appeared in pedigreed laboratory cultures, leaving no doubt about their being typical 'mutants.'

[2] For additional data on the mutants in D. virilis see Metz, C. W., *Genetics, Princeton*. 1916 , 1 (591–607); for data on those in D. melanogaster see Morgan and Bridges, *Washington, Carnegie Inst., Pub.*, No. 237, 1916.

[3] Morgan and Bridges, *op. cit.* 1.

[4] Bridges, C. B., *Genetics, Princeton*, 2 (445–465).

[5] Sturtevant, A. H., *Amer. Nat., Lancaster, Pa.*, 49, 1915 (190–192). Other cases of a similar sort could be added; this one is used because it is taken directly from a Drosophila.

[6] Metz, C. W., *Amer. Nat., Lancaster, Pa.* 50, 1916, (597).

ABSORPTION EFFECTS IN THE SPIRAL NEBULAE

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A study of the negatives of spiral nebulae obtained with the Crossley Reflector has shown that the phenomenon of dark lanes caused by occulting or absorbing matter is much more frequent than had previously been supposed. A paper of considerable length on this subject, in which the evidence is supplied chiefly by half-tone illustrations of seventy-seven spirals, will be published soon by the Lick Observatory. An abstract of that paper follows.